

Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon

James H. Petersen and James F. Kitchell

Abstract: We examined how climatic regime shifts may have affected predation rates on juvenile Pacific salmonids (*Oncorhynchus* spp.) by northern squawfish (*Ptychocheilus oregonensis*, also called northern pikeminnow), smallmouth bass (*Micropterus dolomieu*), and walleye (*Stizostedion vitreum*) in the Columbia River. During 1933–1996, oceanic, coastal, and freshwater indices of climate were highly correlated, and an index for the Columbia River Basin suggested that climate shifts may have occurred about 1946, 1958, 1969, and 1977. Summer water temperature varied as much as 2°C between climate periods. We used a bioenergetics model for northern squawfish, the most important piscivore, to predict that predation on salmonids would have been 26–31% higher during two periods with relatively warm spring–summer water temperatures (1933–1946, 1978–1996) than during an extremely cold period (1947–1958). Predicted predation rates of northern squawfish were 68–96% higher in the warmest year compared with the coldest year. Predation rates of smallmouth bass and walleye on juvenile salmonids varied among climate periods similar to rates predicted for northern squawfish. Climatic effects need to be understood in both freshwater and nearshore marine habitats, since growth rates of salmon populations are especially sensitive to mortality during early life stages.

Résumé : Nous avons examiné comment les changements de régime climatique peuvent avoir affecté les taux de prédation des jeunes saumons du Pacifique (*Oncorhynchus* spp.) par la Sauvagesse du Nord (*Ptychocheilus oregonensis*, aussi appelé le Méné-brochet du Nord), l'Achigan à petite bouche (*Micropterus dolomieu*) et le Doré jaune (*Stizostedion vitreum*) dans le Columbia. De 1933 à 1996, les indices climatiques de l'océan, de la côte et des eaux douces montrent une forte corrélation et un indice calculé pour le bassin versant du Columbia laisse croire à l'existence de changements climatiques vers 1946, 1958, 1969 et 1977. Les températures estivales de l'eau ont subi des variations pouvant atteindre 2°C d'une période climatique à une autre. Un modèle bioénergétique a permis de prédire que, chez la Sauvagesse du Nord, le piscivore le plus important, la prédation des salmonidés aurait été de 26–31% plus élevée durant les deux périodes où les températures de printemps et d'été ont été relativement plus chaudes (1933–1946, 1978–1996) que pendant une période très froide (1947–1958). Les taux prédits de prédation sont de 68–96% plus élevés l'année la plus chaude que l'année la plus froide. La prédation exercée par les Achigans à petite bouche et les Dorés jaunes sur les salmonidés a varié d'une période à l'autre selon les taux prédits chez la Sauvagesse du Nord. Il est donc essentiel de comprendre les effets des changements climatiques, tant dans les eaux douces que dans les habitats marins côtiers, puisque les taux de croissance des populations de saumons sont particulièrement sensibles à la mortalité durant les premiers stades de vie.

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Introduction

Salmon (*Oncorhynchus* spp.) returns to the Columbia River have recently been <2 million adults compared with returns of 8–16 million adults in the early 1800s (National Research Council 1996). Throughout the Pacific Northwest, salmonid species have suffered similar declines (Nehlsen et al. 1991) and 17 stocks have been listed as threatened or endangered

under the Endangered Species Act (<http://www.nwr.noaa.gov/>). The causes for these declines are often ascribed to human activities, including overharvest, habitat destruction from various land-use practices, and construction of dams throughout the basin. Numerous studies have, however, described how natural changes in the ocean environment may have contributed to declining salmon populations in the Columbia River and other basins, especially during the last 70 years (e.g., Francis and Hare 1994; Mantua et al. 1997; Beamish et al. 1999b).

Natural oscillations in climate and ocean conditions in the North Pacific Ocean have occurred on time scales of 2–7 and 20–30 years, and a poorly resolved 50- to 75-year period (Ware 1995). Short-term changes are associated with the El Niño/Southern Oscillation phenomenon, while the 20- to 30-year pattern has been called the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) or climate “regimes” (Beamish et al. 1999b). The PDO in particular has been correlated with temporal and latitudinal changes in salmon production,

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with salmon catch in the Pacific Northwest being higher during periods when the PDO is negative and lower during periods with positive PDO (Francis and Hare 1994; Mantua et al. 1997). The salmon catch in Alaska has tended to be out of phase with the catch in the Pacific Northwest (Hare et al. 1999). Timing of ocean entry, competition for food, temperature-limited growth, and predation on juveniles are some of the mechanisms regulating salmon production that might be affected by ocean conditions and climate oscillation (Percy 1992).

Climate oscillations in the North Pacific Ocean influence not only the ocean environment but also force changes in weather patterns throughout western North America. Stream discharge, stream flow timing, and snowpack, for example, are well correlated over much of the Pacific Northwest, and such environmental variables are driven by large-scale atmospheric patterns (Cayan and Peterson 1989; Cayan et al. 1999). Cayan and Peterson (1989) found that stream flows in the Pacific Northwest were correlated with positive sea level pressure anomalies over the central North Pacific Ocean. Precipitation patterns in western North America are linked to decadal changes in atmospheric circulation and sea surface temperature anomalies on scales that range from regional to global (Cayan et al. 1998). The PDO and April–September flow on the lower Columbia River have been well correlated for 1900–1997 (Hamlet and Lettenmaier 1999), even though dams have influenced flows in the lower Columbia River since the late 1930s.

In this paper, we examined how climate and water temperature in the Columbia River varied between 1933 and 1996 and how temperature changes may have influenced predation rates on juvenile salmonids. Predation occurs throughout the mainstem Columbia and Snake rivers, with especially high losses occurring near dams and in the lower Columbia River (Ward et al. 1995; Beamesderfer et al. 1996). The major piscivores are northern squawfish (*Ptychocheilus oregonensis*, also called northern pikeminnow), smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*), and channel catfish (*Ictalurus punctatus*) (Rieman et al. 1991; Vigg et al. 1991), with only northern squawfish being native to the Columbia River Basin. Northern squawfish, smallmouth bass, and walleye have been estimated to consume 7–17% of all salmonids that annually migrate through John Day Reservoir on the Columbia River (Petersen 1994), and northern squawfish alone may consume 16 million juvenile salmonids annually, 8% of the annual smolt outmigration (Beamesderfer et al. 1996).

Materials and methods

First, we compared three indices of climate to define periods of consistent climate conditions for the Columbia River Basin. Second, we partitioned and tested the differences in water temperature based on the observed climate periods. Finally, we conducted bioenergetic simulations to estimate the predation potential by northern squawfish and other piscivores under different climate and water temperature regimes.

Climate periods or regimes in the Columbia River Basin

Three indices of climate conditions were compared, the PDO index (Mantua et al. 1997), the Pacific Northwest Index (PNI) (Ebbesmeyer and Strickland 1995), and an index specific to the

Columbia River Basin, which we call the Columbia Basin Index (CBI). The PDO is a normalized index based on North Pacific sea surface temperature (Mantua et al. 1997). The PDO was downloaded on May 22, 2000 from web site <http://www.iphc.washington.edu/staff/hare/html/decadal/post1977/pdo1.html>. The PDO has been shown to correlate well with several other indices of climate and adult salmon landings in the North Pacific Ocean (Mantua et al. 1997). The PNI combines air temperature at Olga in the San Juan Islands, total precipitation at Cedar Lake in the Cascade Mountains, and snowpack depth on Mount Rainier. PNI values were obtained on April 28, 2000 from web site http://www.cqs.washington.edu/data/pni_ascii.html.

Because neither the PNI nor the PDO was developed specifically for the Columbia River Basin, we derived an index based on unregulated stream flows within the Basin. We used data from the Hydro-Climatic Data Network (HCDN) (Slack and Landwehr 1992) to derive a CBI of regional climate. The HCDN includes U.S. Geological Survey data from streams and rivers that have not been influenced by watercourse regulation (dams, etc.), irrigation diversions, groundwater pumpage, or land-use change (Slack and Landwehr 1992). Gage records used were within the boundary of the Columbia River Basin, covered 1938–1999, and had <3 years of missing data for an individual gage. Only one gage record was used per watershed (minimum drainage area 1000 km²).

The CBI was the average of normalized flow ((monthly average – long-term average)/standard deviation of the long-term average) across all 19 selected stations (Fig. 1) in the Columbia River Basin for a particular month. Principal components analysis of normalized discharge was used to evaluate whether there were intrabasin patterns among stations. Smith (2000) used a similar protocol to standardize stream flows in British Columbia. Climate periods were identified by examining time series of the PDO, PNI, and CBI (May–August indices). Shifts from positive to negative or vice versa, and a consistent index for periods of >5 years, would suggest a significant change in Basin climate. We also made cumulative sum plots of the CBI (CuSum), which assist in identifying shifts in time series of climatic indices (Beamish et al. 1999b).

Water temperature in the Columbia River

For bioenergetics modeling and related hypothesis testing, we used long-term temperature series collected at Bonneville Dam (1938–1996) and Rock Island Dam (1933–1996) on the Columbia River (Fig. 1). These are the two longest time series of water temperature available for the Columbia River (www.streamnet.org), and they represent an upper and a lower river site. Water temperature was monitored in the dam forebays near turbine intakes (scrollcase); temperature measurements were taken at ~14 m at Bonneville Dam and ~5 m at Rock Island Dam. We assumed that the Rock Island Dam temperatures characterized the upper reaches of the Columbia River (Quinn et al. 1997). Bonneville Dam (river mile 154.5) temperatures were biased high when compared with temperatures measured at Warrendale below the dam (river mile 141.0, U.S. Geological Survey Station No. 14128910, average difference +0.6°C across all months, 1978–1991). We therefore adjusted the long-term Bonneville Dam record for each date between 1938 and 1996 using the average monthly difference between Bonneville Dam and the Warrendale gage.

To test for climate period and location (Bonneville versus Rock Island) effects, we divided water temperatures into three “seasons”: April 1 – May 31, June 1 – August 15, and August 16 – October 31. The April 1 – May 31 season corresponds to increasing flow, slowly increasing water temperature, and outmigration of juvenile sockeye salmon (*Oncorhynchus nerka*), spring chinook salmon (*Oncorhynchus tshawytscha*), and steelhead (*Oncorhynchus mykiss*) in the Columbia River. The June 1 – August 15 period corresponds to decreasing flow, rapidly increasing water temperature, and outmigration of fall chinook salmon. The August 16 – October 31 pe-

Fig. 1. Columbia River Basin and location of climate index and temperature data sites (Bonneville and Rock Island dams) on the Columbia River. Nineteen HCDN stream flow gages (●) were used to compute the CBI of climate. The Columbia and Snake rivers are shown as heavy lines.



riod corresponds to peak and declining temperature, low flows, and few juvenile salmonids in the system.

Analysis of variance (ANOVA) tests of temperature change were conducted on daily anomalies, the differences between a daily temperature and the long-term average temperature on that day and location. Use of temperature anomalies removed trends present within a season, and tests focused on deviations from the long-term average. If a significant model effect was detected ($P < 0.05$), Tukey's multiple range test was used to compare means.

Bioenergetic simulations

Bioenergetics modeling is a proven tool for studying predation rates, temperature effects, and other processes (Kitchell et al. 1977). The model that we applied uses a mass balance approach where growth (G) is equal to consumption (C) minus respiration (R) and excretory losses (E): $G = C - R - E$. Individual terms on the right side of the equation are expanded based primarily on fish size, activity, and water temperature. Fish in different habitats can be modeled by varying diets, while food availability is adjusted with a fit parameter, called a p value, which is the proportion of maximum ration. The sensitivity, merits, and constraints of bioenergetics models have been examined in detail (e.g., Bartell et al. 1986). Bioenergetics models have been shown to be especially useful for evaluating variations in temperature (Shuter and Post 1990).

For northern squawfish, predation was simulated using the bioenergetics model, parameters, and assumptions described in Petersen

and Ward (1999). We modeled an individual fish that was 8 years old, had a starting mass of 668 g, and grew between April 1 and October 31. Northern squawfish that consume juvenile salmonids range in size from ~200 g (~250 mm fork length, age ~5 years) to >2000 g (>500 mm fork length, age 15 years or older), and an 8-year-old fish represents a medium-sized predator in the population. Petersen and Ward (1999) showed that 55% (21 of 38) of the size-frequency distributions of northern squawfish in John Day Reservoir were normally distributed and that populations with slightly skewed weight distributions could be modeled reasonably well with one size-class.

Because we had long-term temperatures from two locations in the Columbia River, Bonneville Dam and Rock Island Dam, we modeled fish representing two general reaches, upper versus lower river. We varied diet to model three types of habitat: a midreservoir habitat, a near-dam habitat (tailrace or forebay), and the free-flowing portion of the Columbia River below Bonneville Dam. Various studies have shown how northern squawfish diets vary among these types of habitat (e.g., Poe et al. 1991). The diet of predators in the free-flowing habitat below Bonneville Dam was based on collections made in that reach, while diets for the other two habitats derive from John Day Reservoir studies (Poe et al. 1991; Petersen and Ward 1999). Although forebay and tailrace near-dam habitats are physically dissimilar, these areas were combined in model runs, since predators in both of these habitats have a relatively high percentage of juvenile salmonids in their diet

(Petersen and Ward 1999). Daily temperature in all simulations was interpolated from average monthly temperature for a particular period.

Swimming speeds in the three habitat types were $1.3 \text{ cm}\cdot\text{s}^{-1}$ (free-flowing and midreservoir habitats) and $7.0 \text{ cm}\cdot\text{s}^{-1}$ (near-dam habitat). The near-dam speed is a compromise of speeds applied by Petersen and Ward (1999): $9.2 \text{ cm}\cdot\text{s}^{-1}$ for a tailrace and $5.0 \text{ cm}\cdot\text{s}^{-1}$ for a forebay. Swimming speeds are based on studies of radio-tagged northern squawfish in the Columbia and Snake rivers (Martinelli and Shively 1997; J.H. Petersen, unpublished data).

We do not know how prey availability and predator diets might have changed during the last 70 years in the Columbia River, so we used two alternative assumptions for modeling growth. First, we assumed that predator growth increments in the past were the same as recent increments or that predators would adjust their food intake to achieve a fixed growth. For these simulations, the predator started at 668 g and grew to 813 g during the season. In a comparable set of simulations, we assumed fixed food availability and allowed the growth rate of the predator to vary. We fit the model p value for the first climate period (1933–1946, see Results) in each reach habitat simulation and used this p value for the other periods. With this approach, consumption of salmonids was the same during the earliest climate period for both the fixed growth and the fixed food availability simulations in a reach habitat.

Variation in stream flow, precipitation, snowmelt, and temperature between years may be considerable depending on short-term phenomena such as El Niño events (Cayan et al. 1999). Using the average daily temperature in July, we determined the warmest and coolest year for the upper and lower reaches and compared cumulative consumption of juvenile salmonids in near-dam habitats between these extreme years.

Finally, we compared salmonid consumption between northern squawfish and two other important piscivores in the system, smallmouth bass and walleye (Vigg et al. 1991), using the bioenergetic formulations and parameters of Roell and Orth (1993) (smallmouth bass) and of Kitchell et al. (1977) (walleye). We used diet summaries for all three predators in John Day Reservoir (Poe et al. 1994) and applied temperatures from both Rock Island and Bonneville dams. All piscivores in these simulations grew from 668 to 813 g between April 1 and October 31. Simulations for each predator species included a loss in mass during spawning.

Results

Climate periods in the Columbia River Basin

Average discharge at selected gages in the Columbia River Basin ranged from 62 to $2472 \text{ m}^3\cdot\text{s}^{-1}$. Smaller drainage basins had somewhat high variations in flows, as expected. Principal components analyses of normalized flows for May, June, July, and August showed relatively high correlations among gaging stations, with no obvious outliers when stations were plotted on principal components axes. The first two eigenvalues explained from 76% (May) to 82% (July) of the total variation in normalized flows. We retained all 19 stations within the basin for index development.

Oceanic, coastal, and Columbia River Basin indices of climate varied in a similar fashion for the period 1933–1996, although there were some obvious differences after about 1980 (Fig. 2). The PNI and PDO were strongly correlated (Pearson's correlation coefficient (τ) = 0.69, $P < 0.001$, $n = 64$). For the months of May, June, July, and August, the CBI was negatively correlated with the PNI ($\tau = -0.42$ to -0.67 , $P < 0.001$, $n = 64$) and also with the PDO ($\tau = -0.27$ to -0.48 , $P < 0.04$, $n = 64$, years 1933–1996).

Time series of the indices showed distinct and coherent shifts between positive and negative values (Fig. 2), suggesting several concurrent climate changes in the North Pacific Ocean, the coastal zone, and the Columbia River Basin between 1933 and 1996. A strong shift in all indices occurred in 1945–1946, when the PNI and the PDO went from positive to negative and the CBI switched from negative to slightly positive (Fig. 2). The period of 1947–1958 had higher than average stream discharges in the Columbia River Basin during May–August. From about 1959 to 1968, the PNI was near zero, while the CBI varied from slightly negative (May) or positive (June) to mixed (July and August). From 1969 to 1977, the PNI was negative, suggesting cool, wet weather, while the CBIs were consistently positive, suggesting higher than average stream flows in spring through summer. In 1977, the PNI shifted dramatically to indicate warmer and dryer weather in the coastal areas of the Pacific Northwest (Fig. 2), while the CBI stream flow indices showed a more complex pattern. Normalized stream flows declined in most months during 1977–1980, increased in 1980–1984, decreased to below-average flows during 1985–1995, and then showed above-average flows in 1996–1999.

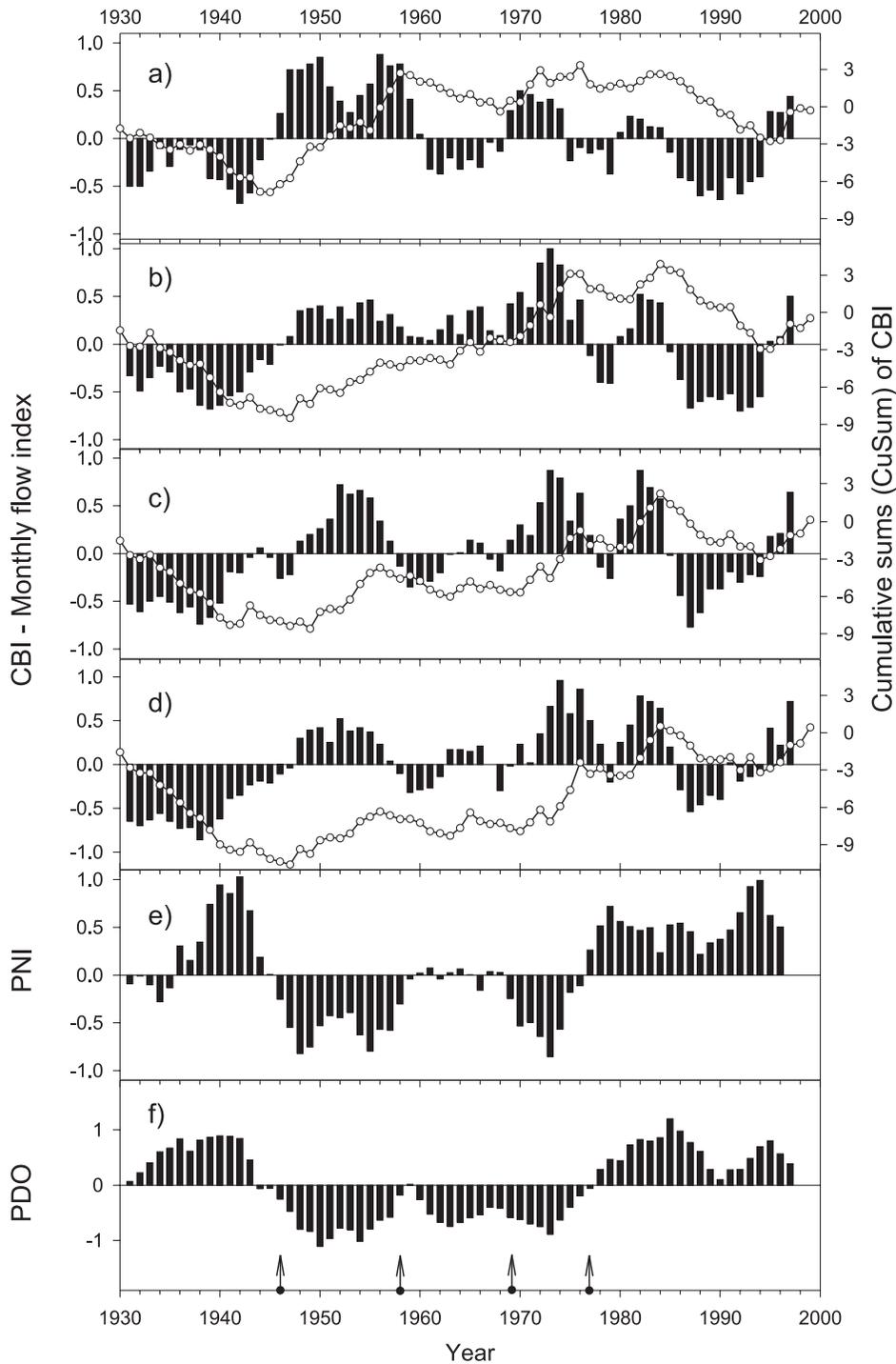
The patterns observed in climate indices (Fig. 2) between 1933 and 1999 suggested that there were roughly four times when climate conditions may have shifted from “high flows” to “low flows” in the Columbia River Basin. We used these four times to divide the overall period into five intervals for temperature analysis (Table 1). We recognize that there are several short-term variations in the stream flow indices that could further divide this period (especially for the years 1980–1999); however, we were interested primarily in longer (>5 years) climatic shifts that were also recognizable in the nearshore marine and ocean environments.

Water temperature

Average July water temperatures, shown as an indicator of short-term variability and long-term trends (Fig. 3), differed by as much as 2°C annually and as much as 4°C over a 4-year period (1955–1959). At both dams where temperatures were recorded from 1938 to 1996, water was relatively warm in the 1930s, cooler in the late 1940s to 1950s, and gradually warmed from about 1960 to 1996 (Fig. 3). The temperature difference between the upriver and downriver sites, Rock Island and Bonneville dams, was fairly consistent for July.

Temperature anomalies were significantly different among climate periods for each location-by-season test (six ANOVAs, all $P < 0.001$). Fifty-two of 60 pairwise comparisons were significant ($P < 0.05$, results not shown), suggesting considerable differences in water temperature among the climate periods within a season (Table 1). At Bonneville Dam, the pattern of temperature change was fairly consistent among the seasons: moderately warm temperatures during 1938–1946, coolest temperatures during 1947–1958, gradually warming temperatures in 1959–1977, and warmest temperatures for the period 1977–1996 (Table 1). Water temperature during April 1 – May 31 varied $<1^\circ\text{C}$ during the 58-year period, whereas from June 1 to August 15, temperature increased by as much as 2°C between the 1947–1958 period and the recent period (1977–1996). At Rock Island Dam, the pattern was slightly different (Table 1). For April 1 – May 31 and June 1 – August 15, water temperatures were about equal

Fig. 2. Climate indices for the (a–d) Columbia River Basin (CBI), (e) nearshore marine zone (PNI), and (f) North Pacific Ocean (PDO index). CBI plots are shown for (a) May, (b) June, (c) July, and (d) August. Vertical bars are 5-year running averages and line plots in the CBI panels are cumulative sums of yearly indices (CuSum). Vertical arrows along the bottom axis of Fig. 2f indicate times used to divide the 1933–1996 period for temperature testing and bioenergetic modeling (see text).



during the earliest period (1933–1946) and the latest period (1978–1996); in the intervening period (1947–1977), water temperature during April 1 – August 15 was ~1.0–1.5°C lower. During August 16 – October 30, water temperature remained fairly constant from 1933 to 1977 and then increased by ~1.0°C after 1977. Water temperature was higher during spring and summer seasons at Bonneville Dam than

at Rock Island Dam, but fall season temperatures were about equal (Table 1).

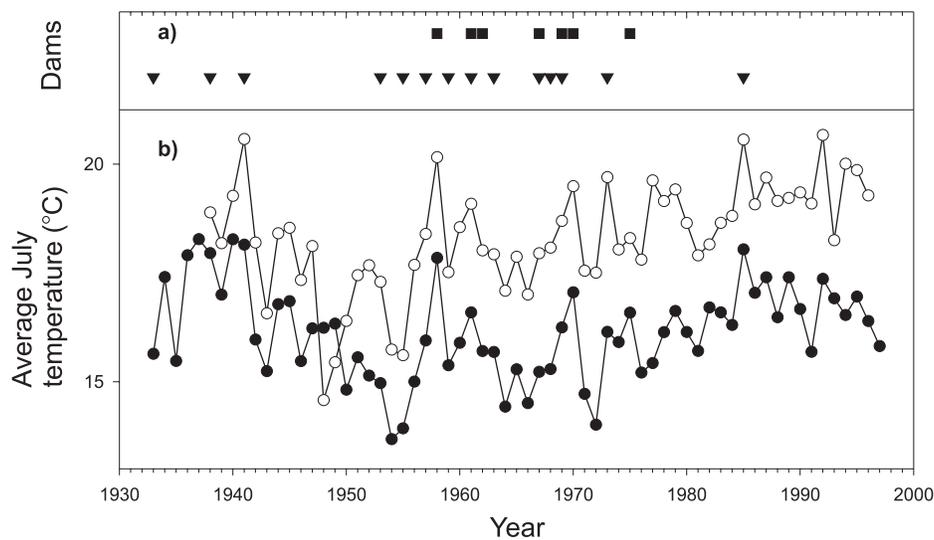
Bioenergetic simulations

In simulations within a given reach and habitat, northern squawfish consumed the fewest salmonids during the 1947–1958 period, consumption of salmonids increased between

Table 1. Average daily water temperature (°C) at Bonneville Dam (1938–1996, adjusted temperatures) and at Rock Island Dam (1933–1996) on the Columbia River.

Period	Bonneville Dam (starts 1938)			Rock Island Dam (starts 1933)		
	Apr. 1 – May 31	June 1 – Aug. 15	Aug. 16 – Oct. 31	Apr. 1 – May 31	June 1 – Aug. 15	Aug. 16 – Oct. 31
1933 or 1938–1946	11.0	17.1	16.2	9.1	15.8	16.5
1947–1958	10.4	16.1	16.2	7.5	14.7	16.8
1959–1969	10.6	17.1	16.8	7.9	14.7	16.4
1970–1977	10.5	17.5	17.2	8.1	14.9	16.8
1978–1996	11.2	18.2	18.0	8.6	15.8	17.8

Note: Temperatures were averaged for three seasons and for five intervals that correspond to climate periods in the Columbia River Basin. Standard errors for all estimates are $\sim 0.1^\circ\text{C}$.

Fig. 3. Average daily water temperature during July at Bonneville (○) and Rock Island (●) dams from 1933 to 1996. Also shown is the year of construction for dams on the lower Snake River (■) and Columbia River (▼, U.S. and Canadian dams).

1959 and 1977, and the highest consumption of salmonids occurred either in the period prior to 1947 or in the period after 1977 (Fig. 4). In the upper river dam habitat (Fig. 4a), consumption of salmonids was about equal in the earliest and the latest period, while consumption of salmonids was $\sim 26\%$ lower during 1947–1958. In the lower river near-dam habitat, consumption of salmonids was highest in the 1978–1996 period, being $\sim 9\%$ higher than during 1933–1946 and $\sim 27\%$ higher than during the cool 1947–1958 period. In the midreservoir habitat (Fig. 4b), the trends were similar to the trends in the near-dam habitat just described. In the upper river, annual salmonid consumption by the simulated northern squawfish varied from a low of 20 g (1947–1970) to a high of 26 g (1933–1946). Consumption was similar in the earliest and latest periods (25 and 26 g). In the lower river, annual salmonid consumption varied from 32 g (1947–1958) to 42 g (1978–1996), a difference of $\sim 31\%$.

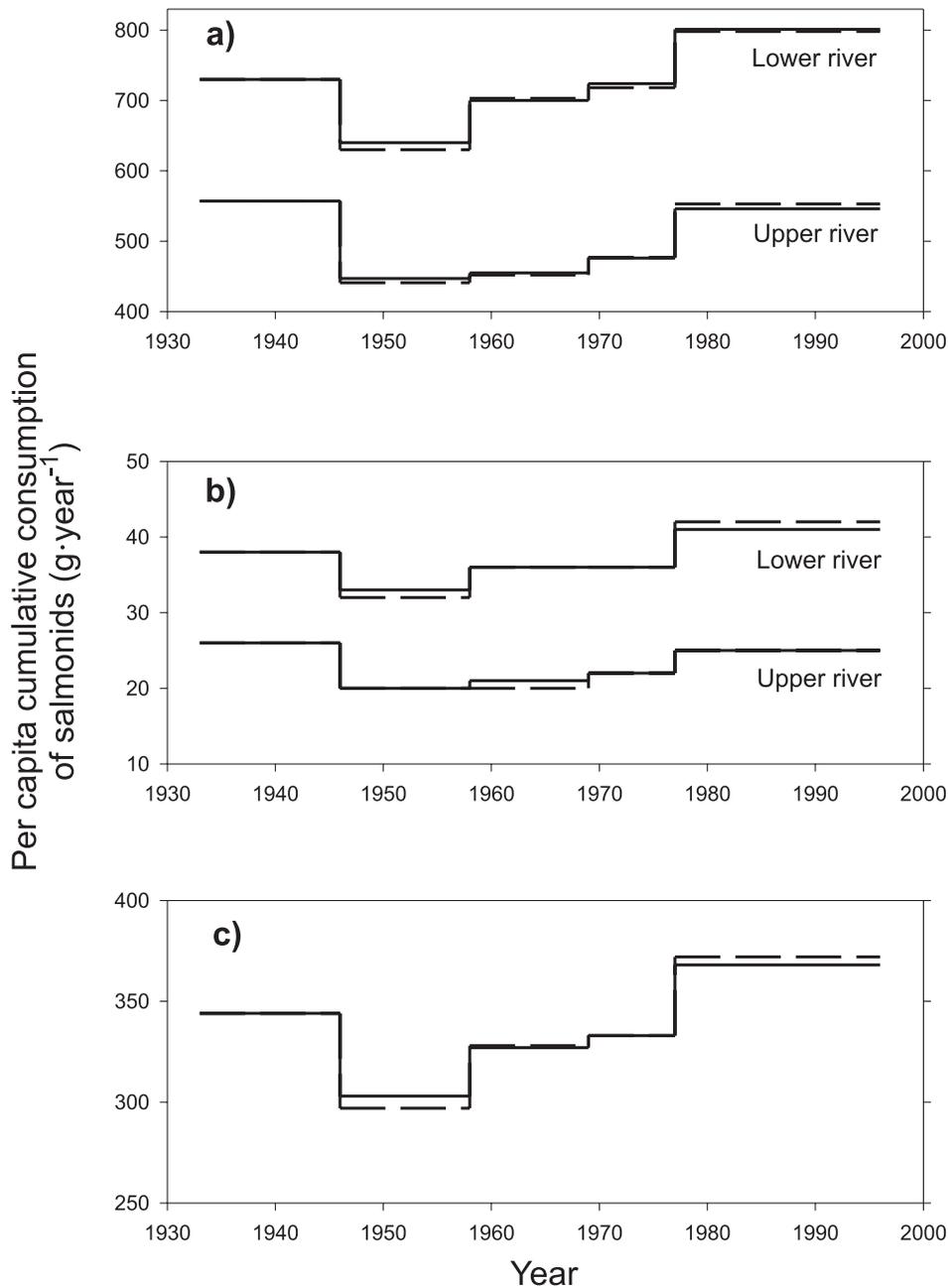
In the free-flowing river habitat below Bonneville Dam (Fig. 4c), predation on salmonids was highest during the 1978–1996 period, being $\sim 26\%$ higher than during the coolest period (1947–1958). Predation on salmonids in this habitat during recent years was predicted to be $\sim 8\%$ higher than during 1933–1946. Allowing growth to vary (fixed food availability) did not produce qualitatively different results from the fixed-growth simulations (Fig. 4). Cumulative

salmonid consumption differed by $<5\%$ between the two different types of simulations. Differences in cumulative annual consumption of salmonids between the habitats (Fig. 4) was caused by different diets used in the simulations and was not related to climate effects. For example, salmonids in northern squawfish were 28–60% of the diet below Bonneville Dam, 28–53% of the diet in near-dam simulations, and 3–9% of the diet for fish in the midreservoir habitat.

Comparisons of potential predation on juvenile salmonids during the coldest and the warmest years between 1933 and 1996 produced dramatic differences. Using Bonneville Dam temperatures, the simulated predator consumed 496 g during the coldest year (1948) and 974 g during the warmest year (1992) (+96%). Using Rock Island Dam temperatures, predation increased from 358 g of salmonids during the coolest year (1954) to 602 g during the warmest year (1937) (+68%).

The three piscivores had similar relative responses to changing water temperature (Fig. 5). Using Bonneville Dam temperatures, the lowest cumulative consumption of salmonids occurred during the 1947–1958 period and the highest consumption occurred during the 1978–1996 period (Fig. 5a). Using Rock Island Dam temperatures, the highest consumption occurred during 1933–1946 (Fig. 5b). Piscivore diet of salmonids varied from low (0–5%, smallmouth bass) to high (45–79%, northern squawfish), causing the mass of salmonids

Fig. 4. Cumulative salmonid consumption simulated for an 8-year-old northern squawfish in three habitats ((a) near-dam, (b) midreservoir, and (c) below Bonneville Dam) in the Columbia River during five climate periods (1933–1996). Near-dam and midreservoir habitats were simulated for temperature regimes in both the upper and the lower river. Simulations also varied according to assumptions about fixed growth (solid lines) or fixed food availability (dashed line) during this period (see text).



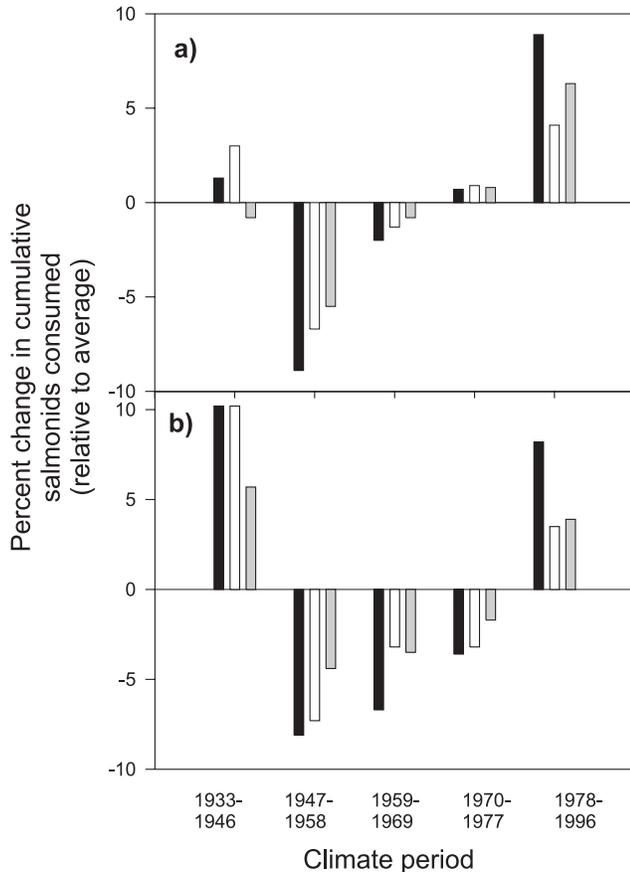
annually consumed to differ greatly between simulated piscivores: northern squawfish (543–649 g salmonids eaten downriver, 407–488 g upriver), smallmouth bass (9–10 g downriver, 7–8 g upriver), and walleye (121–136 g downriver, 104–115 g upriver).

Discussion

Studies on other species have shown how fish distributions, recruitment, or growth often correlates well with climate conditions and water temperature. Shuter and Post (1990),

using bioenergetic arguments, concluded that the northern distributional limits of yellow perch (*Perca flavescens*) and Eurasian perch (*Perca fluviatilis*) are regulated by climate and may shift north with a warming climate. Elliott et al. (2000) observed a close correlation between the emergence timing of brown trout (*Salmo trutta*) and an index of climate from the North Atlantic Ocean. Walters and Ward (1998) suggested that declines in marine survival rates for steelhead, coho salmon (*Oncorhynchus kisutch*), chinook salmon, and Atlantic salmon (*Salmo salar*) may be related to climate changes, particularly increased exposure to ultraviolet radia-

Fig. 5. Percent difference (relative to the overall average) in cumulative per capita consumption of salmonids in the Columbia River by northern squawfish (solid bars), smallmouth bass (open bars), and walleye (gray bars). Estimates were made using bioenergetics models and water temperature from the (a) Bonneville and (b) Rock Island dams.



tion during freshwater residence. Water temperature controls a wide variety of processes in the early life history of salmonids, such as days to hatch and emergence, feeding rate, and growth rate (e.g., Beacham and Murray 1990).

Our analyses suggested that large-scale climate oscillations, or regime shifts, have likely caused water temperature in the Columbia River to vary several degrees between 1933 and 1996. Since feeding by freshwater piscivores is temperature dependent, predation-related mortality of juvenile salmonids has probably varied due to natural climate change. Life table sensitivity analyses for chinook salmon suggested that increasing survival during the first year of life produces the largest increase in λ , the population growth rate (e.g., Emlen 1995). For seven index stocks of spring chinook salmon, a 10% reduction in mortality during the first year resulted in a 41.5% increase in λ (National Marine Fisheries Service 2000). Predation loss of juvenile salmonids in the mainstem Columbia and Snake rivers likely varies 25–30% between the warmest and coldest climate periods and by as much as 96% between the warmest and coldest years. Bradford (1995), in a review of Pacific salmon survival rates, concluded that both freshwater and marine habitats contribute roughly equally to the interannual variability in total

mortality. Thus, the effects of climate change in freshwater may significantly alter first-year survival, with consequences for population growth rates, stock recovery, and management.

Unregulated stream flow, used for our basin index (CBI), has often been used to describe climate changes or trends (Cayan and Peterson 1989; Lins and Slack 1999). A major advantage of using the HCDN data for CBI was that indices were independent of dam construction, irrigation withdrawals, and other watercourse changes that have been extensive in the Columbia River Basin. Trends in the CBI should reflect differences in overall climate and processes regulating stream flow such as precipitation, air temperature, and snowmelt rather than human-caused changes. A second advantage of the CBI for our purposes is that water temperatures in streams and rivers are generally well correlated with flow (e.g., Quinn et al. 1997). June–July flow and temperature were negatively correlated at four dams on the Columbia and Snake rivers ($P < 0.001$; Quinn et al. 1997). Finally, stations used to compute the CBI were broadly distributed throughout the Columbia River Basin, whereas the PNI uses only three stations and characterizes conditions in the nearshore marine environment and on the western slope of the Cascade Mountain Range.

The primary shifts in climate conditions that we used for temperature and energetic analyses, especially changes in 1946 and 1977, were consistent with regime shifts identified in other studies. During the last 100 years, the most well-defined shifts in climate conditions in the North Pacific Ocean and western North America occurred in about 1925, 1947, and 1977 (Ware 1995; Beamish et al. 1999b). Length of day, the Aleutian low pressure index, land and sea surface temperatures, and chlorophyll *a* are some of the correlates used to identify the timing of these climate shifts (Beamish et al. 1999b).

Although major climate shifts were apparent in all indices, the three climate indices that we compared differed in several ways. The PNI and the CBI suggested that weaker climate shifts might have occurred in the coastal and inland areas about 1958 and 1969, while such changes were not as apparent in the PDO index. The strongest differences among the indices occurred from about 1977 to 1999. The positive CBI during spring and summer from 1981 to 1986 was probably the result of the strong El Niño event of 1982–1983 when water flows were greatly above normal (Piechota et al. 1997). Finally, the index of stream flows (CBI) shifted from below-normal flows for about 1985–1992 to above-normal flows after 1993. This change in the CBI in the early 1990s may be an indication of one of the stronger, long-term shifts in the climate such as the 1977 shift (Beamish et al. 1999a). Future studies might further investigate differences in oceanic and stream flow indices and test for correlations between stream flow indices and measures of adult salmon return to the basin.

Changing water temperature may affect salmonid mortality by directly influencing the feeding rate of piscivores and indirectly by affecting the growth rate of predators. Increased temperature during warm periods would cause faster growth of predators, larger size-at-age, and higher juvenile salmonid mortality, since larger predators consume disproportionately more salmonids than smaller predators (Vigg et al. 1991).

Demonstrating such indirect effects of temperature change on growth or other processes that are susceptible to many factors would be difficult, although the mechanisms that we have suggested appear quite plausible.

Our modeling required several assumptions about prey availability, diet, and predator movement. Our assumption of either fixed growth or fixed food availability had relatively little influence on the quantitative or qualitative outcome of the simulations that we ran. We also assumed a constant diet for predators, although diet has probably changed since the 1930s. For example, American shad (*Alosa sapidissima*) became established in the Columbia River in 1895 and their numbers increased dramatically in the lower Columbia River starting about 1958 (Quinn and Adams 1996). Since 1990, 2–3 million adult American shad have passed Bonneville Dam annually to spawn in the Columbia and Snake rivers. Juvenile American shad occur in the diet of northern squawfish and may supplement the growth of predators during late summer and fall (Petersen et al. 1994; J.H. Petersen, unpublished data). Other changes in predator diet could be related to impoundment following construction of hydroelectric dams or to changes in populations of piscivores (Poe et al. 1994). Finally, long-distance movements by predators could expose them to different temperature regimes. Radiotelemetry studies with northern squawfish and smallmouth bass suggest that individuals may migrate considerable distances to spawn, but they generally return and remain in the same general area after these reproductive movements (Martinelli and Shively 1997; J.H. Petersen, unpublished data).

No long-term population data are available for northern squawfish or other predators in the Columbia River, so we used a single hypothetical individual in our simulations. Thus, our estimates of the effects of temperature and climate change on predation were made on a per capita basis and do not reflect any changes in the size of predator populations that may have occurred since the 1930s. Impoundment of the river system has increased the area of certain habitats, perhaps leading to increased or decreased predator populations. The density of northern squawfish is high in tailraces and forebays of dams (Ward et al. 1995), so dam construction since 1933 might have increased the total available habitat and the predator population. On the other hand, fairly high densities of northern squawfish were recently observed in free-flowing reaches of the Columbia River (Hanford Reach) and the lower Snake River (J.H. Petersen, unpublished data), suggesting that impoundment may not have greatly changed the total number of northern squawfish in the system. Predaceous smallmouth bass, walleye, and channel catfish were introduced into the river system prior to 1900, and their numbers likely increased concurrent with impoundment of the river, although we have no long-term population estimates to confirm this (Poe et al. 1994).

Climate changes suggested by the three indices coincided with major dam building efforts on the mainstem Columbia and Snake rivers beginning in 1933, making it difficult to know exactly how much of the predicted predation differences among periods was due to climate shifts rather than impoundment of the system. Most of the dams on the Columbia and Snake rivers are “run-of-the-river” dams with little storage capacity and flushing rates of <4 days. Jaske and Goebel (1967) and Jaske and Synoground (1970) concluded

that the erection of low-head dams on the Columbia River (prior to 1970) produced only a minimal increase in the average temperature of the river. Average June–July temperatures in the Columbia River during 1954–1990 were significantly correlated with temperatures in the Fraser River in British Columbia ($P < 0.01$; Quinn and Adams 1996). Since the Fraser River has not had extensive hydroelectric development, this correlation suggests regional temperature control through snowmelt, tributary warming, precipitation, and other large-scale climate-related processes. The most significant temperature effect of impoundment in the system may be extension of the warmwater period: earlier warming and later cooling within a year (Quinn and Adams 1996; Quinn et al. 1997). At Bonneville Dam on the lower Columbia River, for example, 15.5°C water occurs ~30 days earlier in the spring and remains ~17 days later in the fall, based on data from 1950 to 1993 (Quinn and Adams 1996). Earlier warming and later cooling of water within a year in the impounded Columbia River is accounted for in the model estimates of predation rate, since we used average monthly temperatures per climate period.

The annual hydrograph has obviously been modified by construction of dams, with lower spring and summer flows after impoundment (Ebel et al. 1989), but flow still varies considerably from year to year and presumably modulates water temperature. For example, average June flow varied from 3511 to 13 620 m³·s⁻¹ on the Columbia River at The Dalles Dam for 1973–1994. It is difficult to correlate year-to-year temperature changes with the timing of dam construction, especially since there are both increases and decreases in these temperatures over a few years. The most dramatic change in the Columbia River occurred between 1955 and 1958 when the average daily temperature increased over 4°C. Only two dams, Chief Joseph (1955, flushing rate 2.6 days) and The Dalles (1957, flushing rate 1.1 days), came into service on the Columbia River during this 4-year period (Ebel et al. 1989). Beginning about 1975, summer water temperatures throughout the Columbia River have risen fairly steadily (Quinn et al. 1997), suggesting broad-scale climate effects, since all dams were operational by the early 1970s, except Revelstoke Dam in British Columbia, completed in 1984. Additional analyses of dam and climate effects on water temperatures in the Columbia River Basin would be helpful, perhaps using temperature models driven by local weather conditions.

We limited our analyses to climate regime shifts during the last 70 years, but future trends in global temperature or short-term events could increase predation loss in the Columbia River. Hamlet and Lettenmaier (1999) used two global climate models and a Columbia River hydrology model to predict changes in flow over the next 100 years. By 2045, for example, they predicted a reduction in summer flow at The Dalles Dam of 11–25% and an increase in summer air temperature of 1–3°C, the variation depending on which global model was used. Such flow and air temperature changes might translate into significant changes in water temperature and predation losses. Superimposed on this gradual warming trend are the shorter scale fluctuations of climatic regimes and El Niño events (Hamlet and Lettenmaier 1999). Co-occurrence of a warm climate regime and low flows from an El Niño event, combined with gradual global warming, might

produce especially high water temperatures for a period and high predation losses for juvenile salmonids.

In conclusion, we demonstrated how an important source of mortality for juvenile salmonids, freshwater predation, could be influenced by water temperature changes driven by climatic regime shifts. Predation may also be important to salmonids in estuarine and nearshore ocean environments (Pearcy 1992), further emphasizing the need to understand climate phenomena at large spatial scales. Models that link the ocean, atmosphere, hydrology, and temperature are becoming available (e.g., Hamlet and Lettenmaier 1999) and perhaps can be combined with mechanistic models of predation and salmon movements (e.g., Zabel et al. 1998; Petersen and DeAngelis 2000) to make useful predictions about mortality and population recovery.

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